Early Natural History of the Greater Glider, *Petauroides volans* (Kerr, 1792)

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Maloney, K.S. and Harris, J.M. (2008). Early natural history of the greater glider, *Petauroides volans* (Kerr, 1792). *Proceedings of the Linnean Society of New South Wales* **129**, 39-55.

Early accounts of the greater glider *Petauroides volans* (Marsupialia: Pseudocheiridae) are reviewed, starting with Arthur Phillips' 1789 account in *The Voyage of Governor Phillip to Botany Bay* and proceeding to the latest taxonomic works. This species has a quite complicated and confusing taxonomic history. It has been listed as a member of no fewer than 10 genera with about 23 different binomial names since its discovery. In this paper, we review some of this taxonomic complexity and early descriptions of the species' morphology, dentition, behaviour, distribution and abundance. We found that taxonomic descriptions of *P. volans* have been frequently confused with those of a number of other gliding possums, particularly the yellow-bellied glider *Petaurus australis*. Early descriptions of the morphology of *P. volans* were given only in broad general terms. More value can be placed on the early behavioural observations, and on the earliest records of its occurrence. This paper examines some of the oldest accounts of *P. volans* and assesses their significance.

Manuscript received 14 Februry 2007, accepted for publication 12 December 2007.

KEYWORDS: natural history, nomenclature, *Petauroides volans*, Pseudocheiridae.

INTRODUCTION

The greater glider, *Petauroides volans* (Marsupialia: Pseudocheiridae), is the largest gliding marsupial and is endemic to eastern mainland Australia (McKay 1995). Currently, there are two recognised sub-species: *P. volans volans*, which occurs in south eastern Australia (from Victoria in the south, through mainly coastal New South Wales (NSW) to the Rockhampton district in north-east Queensland (Qld)); and *P. v. minor*, which occurs in very far north-east Qld (from the Dawson River to the Barron River) (Flannery 1994). It is around the size of a domestic cat, with females being larger than males (Flannery 1994; Kavanagh and Wheeler 2004). Most individuals are jet black on the dorsum and creamy white on the ventrum, but pure white forms are not uncommon and intermediate colours are also found (Flannery 1994; McKay 1995; Lindenmayer 2002). This species is nocturnal, arboreal and folivorous and is dependent on tree hollows for its nesting requirements.

Petauroides volans is relatively conspicuous and was quickly noticed by the early colonists (Phillip 1789). Subsequently, descriptions of this species were included in many of the earliest zoological accounts of the Australian fauna. However, few modern zoologists are aware of the historical significance and value of this old literature as it relates to this and other species (see also Harris 2006). Whilst some of this literature on *P. volans* has been reviewed by McKay (1982), this was limited to aspects of the nomenclature of the genus name *Petauroides* (and also *Petaurus*). In this contribution, we have sought to provide a comprehensive survey of the early natural history literature pertaining to *P. volans*, including information on discovery, taxonomy, dentition, morphology, distribution, abundance, diet and behaviour.

TAXONOMY AND NOMENCLATURE

Governor Arthur Phillip reported 'black flying opossum' from NSW (Phillip 1789). A male specimen owned by Henry Constantine Nowell was illustrated (Figure 1), although no details on the precise collection locality were published. Presumably it was found in the vicinity of Port Jackson. Phillip (1789, 1790) recognised that it represented a new species and suggested taxonomic affinity with American

Figure 1: Black flying opossum (=*Petauroides volans*) drawn by P. Mazell and published in Phillip (1789). Note the opposable clawless hallux and syndactylous digits on each of the hind feet.

Didelphis, although a specific name was not offered. A few years later, Kerr (1792) named Phillip's specimen *Didelphis volans*, derived from the Latin word 'volare' meaning 'to fly' (Strahan 1981). A year later, Meyer (1793) named Phillip's specimen *D. voluccella,* and a year later still, Shaw (1794) proposed the name *D. macroura.* In Shaw's work, *The Zoology of New Holland*, a juvenile specimen drawn by James Sowerby was illustrated (Figure 2). Shaw (1800) explained that it was sent to him by John White, who was the first Surgeon-General for the colony of NSW.

Figure 2: Long-tailed opossum *Didelphis macroura* (=*Petauroides volans*) from Zoology of New Holland (1794) by George Shaw. The figure was drawn by James Sowerby. This illustration was also reproduced in Shaw (1800) and Desmarest (1820).

Cuvier (1798) followed use of the name *D. volans* (Kerr 1792) but questioned the affiliation with the genus *Didelphis*. Nevertheless, Shaw (1800) continued the use of *D. macroura*. Bechstein (1800) elevated the name *Voluccella*, used by Meyer (1793), to generic level and proposed *V. nigra* for the subject species, but he evidently confused the greater glider and the yellow-bellied glider *Petaurus australis* in synonymy. His proposed *V. nigra* incorporated *D. voluccella* Meyer, 1793 (=*Petauroides volans*) and "Hepoona Roo" White, 1790 (=*Petaurus australis*). It is understood that Hepoona Roo is *P. australis* and not *Petauroides volans* (McKay 1982, 1988). Bechstein (1800) also advanced *V. macroura* as a separate species that incorporated *D. volans* Kerr, 1792 and *D. macroura* Shaw, 1794. Thus, *V. nigra* and *V. macroura* are both synonyms of *P. volans*. *Voluccella* Bechstein, 1800 was discontinued for the subject species because this genus name had already been advanced by Fabricius (1794) for a species of fly (Diptera: Bombyliidae) (Thomas 1888; McKay 1988; Evenhuis 1991). Hence, *Voluccella* Bechstein, 1800 is a junior generic synonym for *Petauroides* but not *Voluccella* Fabricius, 1794.

Phalanger volans was used by Lacépède (1801), whilst Desmarest (1803) and Tiedemann (1808) placed it under *Phalangista* (see also Schinz 1821; Thomas 1888). Turton (1806) mistakenly thought that the descriptions by Kerr (1792: *D. volans*) and Shaw (1794: *D. macroura*) represented two separate species. Oken (1816) made a similar mistake, but also erroneously included *Petaurus australis* in the synonymy for one of his proposed species. This was *Petaurus niger*, and the epithet was a gender change of Bechstein's (1800) *nigra* (see also Iredale and Troughton 1934). Oken's (1816) second species was *Petaurus macroura*.

Desmarest (1817) listed three species (*Petaurus macrourus*, *P. peronii* and *P. taguanoides*). *Petaurus macrourus* included a slight change in the epithet to standardise the gender of the binomial. Desmarest's explanation that the membrane of *P. peronii* "terminates at the elbow" is good evidence that this specimen was also *P. volans*. For *P. taguanoides* however, the synonymy was confused with the yellow-bellied Glider [i.e. *Didelphis petaurus* of Shaw (1791) and "Hepoona Roo" of White (1790)] and the descriptions about the patagium ending at the wrist suggested to us that this specimen was not the greater glider. However, according to the publications of the Muséum National d'Histoire Naturelle (MNHN) the type specimen of *P. taguanoides* as described by Desmarest is indeed *P. volans* (de Beaufort 1966; Julien-Laferrière 1994). To confirm this identification we contacted the MNHN directly, and obtained a photograph of the specimen (number CG1990-408) and although no patagium was evident in the photograph, it looks like a greater glider because of its substantially long tail and hairy ears. The arrangement of Desmarest's (1817) was later followed by Cuvier (1826), Lesson (1827, 1828, 1830, 1838), and Fischer (1829). Bennett (1837) also used Desmarest's (1817) terminology, although he appears to have used *P. peronii* in reference to the sugar glider *Petaurus breviceps*.

Desmarest (1820) applied *Petaurista* to supercede *Petaurus*, and maintained *Petaurista taguanoides, P. macroura* and *P. peronii* as separate species (later followed by Cuvier 1827, 1829). However, this was flawed as *Petaurista* had been advanced for the giant flying squirrels (Rodentia) by Link (1795) (see also Fischer 1814; Thomas 1888; Sherborn 1902; Palmer 1904). Waterhouse (1838b), Gloger (1842), Gould (1863) and Thomas (1885), persisted with this invalid generic name for the greater glider.

Frédéric Cuvier (1825) mentioned *Petaurus didelphoides* Geoffroy, an apparent new name for the subject species (Thomas 1888; Iredale and Troughton 1934; de Beaufort 1966). However, later works by F. Cuvier and also his brother Georges, made no reference to *P. didelphoides* (Cuvier 1826, 1827, 1829). de Beaufort (1966) noted that Cuvier (1825) offered no specific descriptions, and stated that he was unable to find any reference to Geoffroy as the authority for the name. It is uncertain whether Cuvier intended this name for the greater glider. Iredale and Troughton (1934) considered it a vernacular name.

Lesson (1828, 1830, 1838) listed the "Black Flying Opossum" of Phillip (1789) (=the greater glider) as a junior synonym of *Petaurus taguanoides*. This was subsequently repeated by Fischer (1829), Wagner (1843), Schinz (1844) and Giebel (1859). Waterhouse (1838a) then stated that two specimens of *Petaurista taguanoides* were held in the Museum of the Zoological Society of London (ZSL), one of which was a 'white variety'. Waterhouse's (1841) included an illustration of a greater glider (Figure 3) and stated that "Specimens which are totally white, and others which are white and irregularly variegated with grey, are not rare". Waterhouse (1841) was wrong when he suggested that *P. macrourus* is *P. flaviventer* (=*P. australis*) (see also Wagner 1855; Giebel 1859; Gould 1863). Descriptions of *taguanoides* specimens in many 19th century publications subsequent to Waterhouse (1841) appear to represent the greater glider (e.g. Owen 1841, 1845; Gloger 1842; Waterhouse 1846; Gervais 1855; Gerrard 1862; Brehms 1880; Flower 1884; Forbes-Leith and Lucas 1884; Krefft 1864; Haswell 1886; Jentink 1886; Lucas 1890).

Figure 3: A print from Waterhouse (1841) that is clearly *Petauroides volans* because of the length of the tail and the hairy ears. This image was also reproduced in Waterhouse (1843) and Lydekker (1896).

Major T.L. Mitchell collected a presumed new species of glider "from the banks of the Murray", named it *Petaurus leucogaster* and "deposited [it] in the Australian Museum (AM)" (Bennett 1837; Mitchell 1838). Gray (1841) suggested that it "may only be a variety of [the] *P. taguanoides*" of Waterhouse (=the greater glider) (see also mention of *P. leucogaster* in Gray 1842, 1843; Krefft 1864). Several authors considered *leucogaster* to be synonymous with *P. volans* (Gould 1863; Thomas 1888; Iredale and Troughton 1934; McKay 1982). However, McKay (1988) stated that *P. leucogaster* was 'Incertae sedis' (of uncertain position) because the specimen could no longer be found at the AM. He suggested that the locality for Mitchell's specimen was outside the range of *P. volans* and may have been *Petaurus norfolcensis*.

M.R. Oldfield Thomas, of the British Museum of Natural History (BMNH), revised the taxonomy of the subject species several times during the period 1879-1923. Thomas (1879) noted that the specific name *volans* Kerr antedated *taguanoides* Desmarest, and maintained that the correct binomial was *Petaurus volans*. A few years later, however, he listed it as *Petaurista volans* (Thomas 1885). After finding that *Petaurista* was unavailable, Thomas (1888) advanced *Petauroides* to replace the previous generic names. He listed two subspecies: *Petauroides volans typicus* as the southern form; and *P. v. minor* as the northern form (following Collett 1887). Later, Thomas (1923) received further examples from Qld and considered that there were two additional subspecies: *P. v. incanus* and *P. v. armillatus*.

Thomas (1923) mentioned that Ogilby (1892) referred to "Dr Ramsay's *P. cinereus*" and that it "seems never to have been described". However, Ramsay (1890) did indeed publish a description of a supposed new species, which he named *Petaurides cinereus*. This was based on two specimens obtained from the Bellinden-Ker Range, north-east Qld. The name *Petaurides* is a definite misspelling of *Petauroides* Thomas 1888 (see Ramsay 1890). It is also noted that these specimens had earlier been exhibited at a meeting of *The Linnean Society of NSW* under the name of *Belideus cinereus* (Anon 1890).

The next taxonomic contribution was by Iredale and Troughton (1934). They argued that the generic name *Schoinobates* Lesson 1842 had been published before *Petauroides* Thomas 1888, and advanced the name *S. volans* with four subspecies: *S. v. volans*;

S. v. incanus; *S. v. armillatus* and *S. v. minor*. Subsequently, *S. volans* was in use for around 50 years (Fleay 1947, 1968; Tate 1945; Anon 1946; Troughton 1935, 1941; Marlow 1958, 1962; de Beaufort 1966; Ride 1970; Strahan 1980, 1981). However, the nomenclatural change by Iredale and Troughton (1934) was groundless. McKay (1982) pointed out that *Schoinobates* was first used by Lesson (1842) to supersede *Petaurista leucogenys* Temminck, 1838 (=*Pteromys leucogenys*; the Japanese flying squirrel). In fact, this was an error on Lesson's part because there are no marsupials in Japan (Palmer 1904). Nevertheless, it was highly irregular for Iredale and Troughton to amend the type locality of *P. leucogenys* from "Japan" to "Sydney". Probably, Iredale and Troughton (1934) did not view the original account and illustration of *P. leucogenys* in *Fauna Japonica* (Temminck 1838), which clearly depicts a sciurid. *Schoinobates* Lesson, 1842, is therefore properly placed as a junior synonym of *Petaurista* Link, 1795. Thus, McKay's (1982) assessment that the name *Schoinobates* was unavailable and that *Petauroides* must stand was justified.

Iredale and Troughton (1934) also nominated *Petaurus maximus* as a synonym for the subject species, listing Partington (1837) as the authority. This was accepted by McKay (1982) and Flannery (1994). However, McKay later attempted unsuccessfully to track down the original reference and stated that the relevant page in the book he examined "contains no reference to this or any other mammal" (McKay 1988). We note that McKay (1988) misread Iredale and Troughton's (1934) reference to Partington (1837: 424) because *P. maximus* is indeed described in *The British Cyclopædia of Natural History*, but not in the *The British Cyclopædia of Arts and Sciences*, which was read by McKay (1988). After reading Partington (1837) with its reference to some "almost white" specimens, we accept *P. maximus* as synonymous with the greater glider (following Iredale and Troughton 1934). The preceding literature review of taxonomy of the Greater Glider is presented in Table 1.

Common names for the subject species have included 'black flying opossum' (Phillip 1789), 'flying opossum' (Kerr 1792; Turton 1806; Waterhouse 1841), 'long-tailed opossum' (Shaw 1794, 1800; Turton 1806; Waterhouse 1841), 'large-tailed Petaurista', 'Peron's Petaurista' (Cuvier 1827), 'white-bellied flying squirrel' (Bennett 1837), 'grey flying squirrel' (Bennett 1837; Waterhouse 1841) 'large-tailed flying squirrel' (Bennett 1837), 'taguan flying opossum' (Waterhouse 1838b), 'taguan flying phalanger' (Waterhouse 1846; Thomas 1888, 1923; Fleay 1933), 'greater flying phalanger' (Gould 1863; LeSouef and Burrell 1926; Fleay 1933), 'the brill' (De Vis 1886), 'flying phalanger' (Haswell 1886), 'great flying oposssum', 'flying squirrel' (Lucas 1890), 'dusky glider' (Fleay 1933; Ride 1970), 'greater glider-possum' (Iredale and Troughton 1934; Anon 1946), and 'greater glider' (Marlow 1958). Stability in the vernacular name was achieved in 1980 when a committee of the Australian Mammal Society formalised it as the 'greater glider' (Strahan 1980).

MORPHOLOGY

The morphology was first described by Phillip (1789). He stated that the "tip of the nose to root of tail [was] 20 inches [=508 mm], tail 22 inches [=559 mm], loins 16 inches [=406 mm]." The ears were described as "large and erect", the fur "glossy black" on top, "mixed with grey", and "the under parts...white". It was noted that the fur "continued to the claws", and that the membrane "expanded on each side of the body". Phillip (1789) also described and illustrated the foot (Figure 1). He observed that the "fore legs have five toes on each foot, with a claw on each; the hinder ones four toes, with claws, (the three outside ones without any separation) and a thumb without a claw". Following Phillip (1789), similar descriptions were also published by subsequent authors based on his original account and from the illustration provided (i.e. Kerr 1792; Meyer 1793; Bechstein 1800). Shaw (1794) provided morphological descriptions based on the illustration reproduced in Figure 2.

One diagnostic feature of *P. volans* is the flying membrane that runs from the elbow to the knee, and this was noted by several early zoologists (Kerr 1792; Turton 1806; Desmarest 1817; Waterhouse 1841, 1846). Thomas (1888) added that the membrane is "very narrow along the sides of the forearm and lower leg". Ramsay (1890) stated that the "parachute" or "wing membrane" commences a little in front of the elbow-joint, and extends to about half-way below the knee-joint. Numerous early authors also noted the syndactylous hind feet (Kerr 1792; Shaw 1794, 1800; Bechstein 1800; Lacepede 1801; Tiedemann 1808; Desmarest 1820; Partington 1837).

Some authors have compared the size of this species to animals known from Europe. For example, it has been suggested to be about the size of a "black rat" (Shaw 1800), "flying squirrel" (Desmarest 1803; Tiedemann 1808), "surmulot" (Cuvier 1817; Desmarest 1820; Lesson 1827), "squirrel of Europe" (Desmarest 1820; Lesson 1827), and "brown rat' (Partington 1837). More recently, it has been suggested to be about the size of a domestic cat

Table 1: New synonymy based on the current review.

Petauroides Thomas, 1888
- *Petaurus* Shaw, 1791
- *Didelphis* Kerr, 1792
- *Voluccella* Bechstein, 1800
- *Phalanger* Lacepede, 1801
- *Phalangista* Desmarest, 1803
- *Petaurista* Desmarest, 1820
- *Petauroides* Thomas, 1888
- *Petaurides* Ramsay, 1890
- *Belideus* Anon, 1890
- *Schoinobates* Iredale and Troughton, 1934
  - *Petauroides volans* (Kerr, 1792)
    - *Petauroides volans volans* (Kerr, 1792)
      - *Didelphis volans* Kerr, 1792
      - *Didelphis voluccella* Meyer, 1793
      - *Didelphis macroura* Shaw, 1794
      - *Voluccella nigra* Bechstein, 1800
      - *Voluccella macroura* Bechstein, 1800
      - *Phalanger volans* Lacepede, 1801
      - *Phalangista volans* Desmarest, 1803
      - *Petaurus macroura* Oken, 1816
      - *Petaurus niger* Oken, 1816
      - *Petaurus taguanoides* Desmarest, 1817
      - *Petaurus macrourus* Desmarest, 1817
      - *Petaurus peronii* Desmarest, 1817
      - *Petaurista taguanoides* Desmarest, 1820
      - *Petaurista macroura* Desmarest, 1820
      - *Petaurista peronii* Desmarest, 1820
      - *Phalangista macroura* Schinz, 1821
      - *Petaurus didelphoides* Cuvier, 1825
      - *Petaurus maximus* Partington, 1837
      - *Petaurus volans* Thomas 1879
      - *Petaurista volans* Thomas 1885
      - *Petauroides volans typicus* Thomas, 1888
      - *Petauroides volans incanus* Thomas, 1923
      - *Petauroides volans armillatus* Thomas, 1923
      - *Schoinobates volans volans* Iredale and Troughton 1934
      - *Schoinobates volans incanus* Iredale and Troughton 1934
      - *Schoinobates volans armillatus* Iredale and Troughton 1934
    - *Petauroides volans minor* (Collett, 1887)
      - *Petaurista volans minor* Collett, 1887
      - *Belideus cinereus* Anon, 1890
      - *Petaurides cinereus* Ramsay, 1890
      - *Schoinobates volans minor* Iredale and Troughton 1934

(Flannery 1994).

Colouration was also frequently commented on. For example, Cuvier (1817) reported that the fur exists in different tones of brown, with many varieties, and others are whitish. Fully white specimens were also noted (Lesson 1827; Waterhouse 1841; Krefft 1864; Le Souef and Burrell 1926). Gould (1863) stated that "it is subject to very great variety in the colouring of its fur, some specimens being entirely blackish brown [see Figure 4], grey to cream and others quite white". Krefft (1871) reported that the species "varies much from creamy-white to spotted black and white and

Figure 4: *Petaurista taguanoides* from Gould (1863) (= *P. volans*). Note: The front arms of the background glider are shown in the wrong position as *P. volans* tucks them under the chin when gliding (Fleay 1933; Grzimek 1967; McKay 1989).

Table 2: Dental formulas provided in the early natural history literature for *Petauroides volans*. Abbreviations: I = Incisors; C = Canines; M = Molars; P = Premolars. For Thomas (1885, 1888) an asterisk indicates that the tooth is sometimes or commonly absent.

Source	Dental formula
Desmarest 1820	$I\frac{6}{2};C\frac{1\,1}{0\,0}\,or\,\frac{1\,1}{2\,2};M\frac{6\,6}{6\,6}\,or\,\frac{7\,7}{6\,6}$ = 32 or 34
Cuvier 1825, 1826	$I\frac{6}{2};C\frac{0\,0}{0\,0};M\frac{8\,8}{6\,8}$ = 38
Lesson 1827, 1830, 1838; Fischer 1829	$I\frac{6}{2};C\frac{0\,0}{0\,0};M\frac{8\,8}{7\,7}$ = 38
Waterhouse 1838b	$I\frac{3\,3}{1\,1};C\frac{1\,1}{0\,0};P\frac{3\,3}{1\,1};M\frac{4\,4}{4\,4}$ = 34
Krefft 1871; Collett 1887	$I\frac{3\,3}{1\,1};C\frac{1\,1}{1\,1};P\frac{3\,3}{3\,3};M\frac{4\,4}{4\,4}$ = 40
Thomas 1885	$I\frac{1\,2\,3}{1\,0\,0}C\frac{1}{1*}P\frac{1}{1*}\frac{2\,3}{2*3}M\frac{1\,2\,3\,4}{1\,2\,3\,4}x2$ = 34 or 40
Thomas 1888	$I\frac{1\,2\,3}{1\,2*\,0}C,\frac{1}{0}P,\frac{1}{1*}(or1)\frac{0}{0}\frac{3\,4}{3*4}M,\frac{1\,2\,3\,4}{1\,2\,3\,4}$ = 17 + (at most) 3 (or 16 + 4) × 2 = 40

perfect black, beneath the fur is always white." Le Souef and Burrell (1926) stated that "as a rule [the] colour [is] darker in winter than in summer." They also stated that "animals from Gippsland (Victoria) [were] dead black above and on tail; pure white on undersides", whereas Qld and NSW specimens were "usually smoky grey" and "white specimens [were reportedly] common."

Other notable morphological features described in the early literature include the ears, tail and size differences between the sexes. Waterhouse (1838a, 1841, 1846) stated that "the ears are entirely covered externally with long and dense fur, flesh-coloured and almost bare within" (see also Krefft 1864, Thomas 1888, Ramsay 1890). The tail was reported as not being prehensile (Lacepede 1801; Tiedemann 1808; Partington 1837), and longer than the body (Shaw 1800; Turton 1806; Cuvier 1817). Thomas (1888) described and illustrated the naked tip of the tail. Gould (1863) stated the "sexes offer no external difference, except that the female is somewhat smaller than the male" (see Flannery 1994, as this is erroneous). Various other aspects of the morphology of this species are discussed in the literature, but lack of space precludes a detailed discussion here. However, these aspects include skull structure (Waterhouse 1846; Collett 1887; Thomas 1888) and myology (Haswell 1886).

DENTITION

Phillip (1789) stated that in "the upper jaw forwards are four small cutting teeth, then two canine ones, and backwards five grinders: the under jaw has two long large cutting teeth, five grinders, with no intermediate canine ones, the space being quite vacant". Similarly worded descriptions were provided by Kerr (1792) and Turton (1806).

A dental formula for the species was first provided by Desmarest (1820) (see Table 2). He counted six upper and two lower incisors, but was uncertain about the number of canines and premolars. This uncertainty led him to indicate a total of 32 or 34 teeth. Cuvier (1825) and Lesson (1827) counted a total of 38 teeth. Cuvier (1825) reported that the space between the incisors and molars is occupied by two rudimentary teeth. Waterhouse (1838b, 1841) and Owen (1841, 1845) mentioned they had never observed any of these diminutive teeth in the specimens they had examined. Waterhouse (1841) suggested that Cuvier (1825) may have inadvertently described the dentition of *Phalangista cookii* (=*Pseudocheirus peregrinus*; common ringtail possum). These two species do have great similarity in their dental characteristics, as noted by early zoologists (Owen 1841, 1845; Giebel 1853, 1855; Thomas 1885; Collett 1887) and more modern authors (Tate 1945; Triggs 1996). Waterhouse (1838b) provided a dental formula indicating a total of 34 teeth. Subsequent authors concurred with this

observation (Waterhouse 1841, 1846; Wagner 1843; Collett 1887; Ramsay 1890). Early illustrations of the dentition in Cuvier (1825, 1827), Waterhouse (1846) and Giebel (1853, 1855) support the dental formula of Waterhouse (1838b).

Krefft's (1871) dental formula (Table 2) was for a total of 40 teeth (see also Collett 1887). Thomas' (1885) assessment was that the number of teeth varied from 34 to 40, dependent on the presence or absence of a small canine and two premolars in the lower jaw. Thomas (1888) attempted to improve his earlier dental formula by changing the position of the lower canine to the incisor position (Table 2), and remarked that the "presence or absence of the minute teeth is not of any systematic importance". Thomas (1888) provided illustrations of the upper and lower jaw of *P. v. volans* and *P. v. minor*, although these are not consistent with his dental formula. Later reviewers have alluded to a socket in the lower jaw where a small incisor would be present (i.e. Archer 1984; Triggs 1996). Twenty-one *P. volans* specimens in the AM were recently examined by us, and four (19%) were noted to have minute teeth between the incisors and pre-molars.

HABITAT AND DIET

Some information on the habitat and diet of *P. volans* is available in the early literature. Gould (1863) stated that the species seeks "blossoms of the Eucalypti...together with the tender buds and shoots of the same trees". Similarly, Le Souef and Burrell (1926) stated that the "food consists of the leaves and buds of eucalyptus-trees". They also added that:

> 'careful examination of the contents of several stomachs of animals taken from the forests has not revealed anything else, but in the Myall Lakes district [NSW]... we have observed this species on the casuarina-trees; in one such case the contents of the stomach, although much masticated, seemed to be the casuarina-leaves. Mr. Ralph C. Blackett, forest ranger at Queanbeyan [NSW]..., states that they chiefly feed on *E. regnans*, and to a lesser extent on *E. viminalis*, *E. fastigata*, *E. australasiana*, and other narrow-leaved peppermints.'

In captivity, *P. volans* has been observed to eat *E. sieberiana* readily, "being especially fond of the flowers, and preferring the bark of the branches to the leaves" (Le Souef and Burrell 1926). Fleay (1933) stated "one of the chief difficulties in captivity is the maintenance of an abundant supply of the tender leaves of acceptable species of eucalypts" and reported on collecting trips to obtain sufficient amounts of leaf from *E. elaeophora* and *E. australiana*. He also reported that "captive specimens could be persuaded to acquire an additional taste for bread and milk spread with a sweet jam, but only as an adjunct to the diet of eucalypt leaves." Grzimek (1967) stated "because [*P. volans*] are exclusive in their diet, like koalas, no specimen has ever reached a European zoo alive." Menkhorst and Knight (2004) stated that it "eats only eucalypt leaves and buds." However, Maloney and Harris (2006) report feeding observations from several non-eucalypts.

In terms of habitat, Gould (1863) wrote that it "is strictly an inhabitant of the extensive brushes which stretch along the south-eastern and eastern portions of New South Wales". It has also been reported to occur in *Eucalyptus* forests (Le Souef and Burrell 1926, Anon 1946). Fleay (1933) stated that the species was found "favouring the taller timber areas and generally inhabiting dead trees in the gullies of mountainous country". Marlow (1958) reported that *P. volans* was more abundant in dry than wet sclerophyll forests and less common in open woodland. Ride (1970) stated that "the habitat is sclerophyll forest and tall woodland".

DISTRIBUTION AND ABUNDANCE

The earliest statements on the distribution of the subject species was that it inhabits NSW (Phillip 1789; Kerr 1792) or "New Holland" (=Australia) (Meyer 1793; Shaw 1794; Cuvier 1798; Bechstein 1800). The earliest specific localities mentioned were for places in NSW, i.e. Botany Bay, Port Jackson, Sydney, Blue Mountains, Port Macquarie, Bathurst, Maitland, Clarence River and Goulburn Plains (Cuvier 1826, 1827; Lesson 1830; Bennett 1837; Waterhouse 1841; Gray 1841; Krefft 1864). Other early distributional records for NSW include Sutherland (1908, AM M2003), Helensburgh (1909, AM M2051), Bowral (1918, AM M2724), Myall Lakes (1922, AM M33762), Gerringong and Milton (Troughton 1935, 1941), Geehi Gorge (Mt Kosciuszko area) (Anon 1946), Armidale and Tidbinbilla Nature Reserve (1974), (see Maloney and Harris 2006).

Early literature records from Queensland are north of the Herbert River (de Vis 1886), Herbert Vale, Coomooboolaroo, Calliungal (Collett 1887),

Bellenden-ker Range (Ramsay 1890), Eidsvold, Gin-Gin (Thomas 1923), Atherton Tablelands, Evelyn Station, Dimboola and Mount Spurgeon Stations (Tate 1945).

In Victoria, they have been reported from Templestowe around 1865; east and north-east of Melbourne (Lucas 1890), and also from the south, south-west and questionably north-west areas of the State (Forbes-Leith and Lucas 1884; Lucas 1897). Other Victorian distributional records include Allambee East, Newham, Bullengarook (1905), Dandenong (1923), Mitta Mitta (1931), Upper Beaconsfield, Traralgon, Daylesford, Bendoc (1933); Buchan (1960), Matlock (1961), Healesville, Yellingbo, Powelltown (1963), Woori Yallock, Darlimurla (1966), Upper Thompson Valley (1968), Marysville (1969), Porepunkah, Mount Buffalo and Upper Lerderderg Valley (1970) (see Maloney and Harris 2006).

Gould (1863) believed that its range was from "Port Phillip to Moreton Bay". Krefft's (1864) assessment was that it occurred in the "mountainous coast districts of the Australian continent", from Victoria to Qld; also that it was "not found upon the plains of the interior". Thomas (1888) and Lydekker (1896) reported that its range was from Qld to Victoria. Fleay (1933) stated that the range "extends down the highlands of eastern Australia from southern Qld. to Victoria", and that he had "never observed the species further west than the Ballarat-Daylesford forest" in Victoria. Marlow (1958) found that the western limits of its distribution in NSW were Barraba, Orange and Tumut. Ride (1970) reported the distribution to be from the Dandenong Ranges (Victoria) to Rockhampton, Qld.

In terms of abundance, the species has been described as the "most abundant of the arboreal marsupials in the forests to the east and north-east of Melbourne" (Lucas 1890), "very plentiful in the heavy eucalypt forests" of eastern Australia (Le Souef and Burrell 1926); and "among the most numerous of arboreal marsupials" in East Gippsland (Fleay 1933). Marlow (1958) reported that *P. volans* was "abundant" in NSW (see also Calaby 1966; Flannery 1994; McKay 1995). Currently, *P. volans* is not listed as threatened in the three states that it occurs, and recent distribution maps are provided by Eyre (2004) and Winter *et al* (2004) for Qld, Kavanagh (2004) for NSW and van der Ree (2004) for Victoria.

BEHAVIOUR

The gliding ability of *P. volans* was first reported by Phillip (1789) and then by Shaw (1794, 1800), Cuvier (1798) and Turton (1806). Later authors remarked that it moves with a gliding motion, but this was not true flying (Desmarest 1817; Lesson 1827; Owen 1841, 1845; Lydekker 1896). Le Souef and Burrell (1926) record a "flight by one of these animals from the top of one tall eucalypt to the base of another was 80 yards [=73 m]; another flight, of 55 feet [=17 m], occupied 1 ½ seconds." Troughton (1935, 1941) stated that it is "the record glider of the possum world" and reported that one individual was observed at Milton NSW, covering a distance of 590 yards [=540 m] in six successive glides. Two of these glides were 120 yards [=110 m], and one of 70 yards [=64 m] from a tree 100 feet [=30 m] high. Wakefield (1970) stated "that some long glides, attributed in the literature to *P. volans*, belong in fact to *Petaurus australis*". He discussed the report by Troughton (1935, 1941) and stated:

> 'The 70 yard [=64 m] glide from a 100-foot [=30 m] tree indicates an angle of descent of 26 degrees to the horizontal, and, even allowing for sloping ground and a margin of error in the measurements, this performance, though well within the capabilities of *Petaurus,* is quite outside that of *Petauroides*. Also, for the 120-yard [=110 m] glides *P. volans* would require for its 40 degree descent, a take-off point approximately 300 feet [=90 m] high, while *Petaurus* would need a 200-foot [=60 m] tree. Other features of the Milton resident's report – that during the performance the animal "lost no time in ascending three more trees" and that "it uttered its peculiar squealing call" – leave no doubt that the "record glider" was, in fact, *Petaurus australis* and not *Petauroides volans*.'

The voice and gliding accomplishments of *Petaurus australis* have been credited erroneously to *P. volans,* which is, in fact, a sedentary, slow-moving, silent animal of minor gliding ability (Wakefield 1970; McKay 1989). Many authors have mistakenly accredited *P. volans* with the vocalisations of *P. australis*: for instance Lydekker (1896) was the first to erroneously report "when disturbed, or in flight, they utter a loud piercing scream, audible for a long distance" (see also Le Souef and Burrell 1926; Troughton 1935, 1941; Fleay 1933, 1947; Calaby 1966 for similar reports).

It was also recognised quite early that this species was nocturnally active and utilised tree hollows as den sites during the day (Oken 1816; Desmarest 1817; Lesson 1827; Partington 1837; Waterhouse 1846; Thomas 1885; Collett 1887; Aflalo 1896). Gould (1863) stated that "on the approach of evening [it] emerges from its retreat." Lydekker (1896) reported that they "spend the day in some hollow branch or the stem itself, whence they issue forth for their nocturnal flight".

Le Souef and Burrell (1926) suggested that the only predators of *P. volans* are the powerful owl *Ninox strenua* and the introduced fox *Vulpes vulpes*; 'the latter occasionally catches them on the ground' (see also Fleay 1933, 1947, 1968). However, Maloney and Harris (2006) reported *P. volans* falling prey to a range of other predators such as the cat *Felis catus*, dog *Canis familiaris*, fox *V. vulpes*, wedge-tailed eagle *Aquila audax*, quoll *Dasyurus maculatus* and sooty owl *Tyto tenebricosa*. Other recorded predators of the greater glider include the dingo *C. f. dingo* (Robertshaw and Harden 1985), lace monitor *Varanus varius* (Weavers 1989) and carpet python *Morelia spilota* (Lindenmayer 2002).

Fleay (1933) reported:

> 'Wandering under the trees on a still night, when the dusky gliders [*P. volans*] are feeding overhead, rarely leads to their discovery without resort to intent listening. Perhaps the faint sound of a leaf being pulled from a stalk, or a sudden rustle as the animal plunges its weight from one slender limb to another, betrays its position to a searching torch beam held so that the observer's eyes look straight along the path of light. Then the blazing orbs of the animal, certainly the most brilliant light reflectors that I know of among the marsupial family, regard the intruder with some curiosity'.

In terms of its reproduction and breeding behaviour, Desmarest (1817) reported "females have a pouch under the belly, where the young spend the first part of their existence". Fleay (1933) made the following observations on captive specimens: "only two mammae are found in the pouch" and "only one embryo is reared at a time." He also reported as follows:

> 'In Vic. this minute naked creature seems to appear usually in July or August, and it is difficult to realize that such a mite, no larger than the head of a drawing-pin, may indulge some day in graceful aerial "flights". Gradually as the youngster increases in bulk, it is noted that the limbs and tail are extraordinarily long, the loose volplaning membrane from fore limb to hind limbs is plainly visible, and the colour of the furless embryo is pink with very dark ears. The little fellow becomes free of its inseparable attachment to the mamma when some six weeks of age. Later the eyes open and a covering of short fur indicates plainly the contrast between the black and white of the upper and lower surfaces respectively. It then spends the daylight hours out of the pouch, and by night is carried around as a large bulge in it. At four months it has become too bulky to be contained in the pouch any longer. Between the growing of fur and the forsaking of the mother's "pocket nursery" the young Taguan Phalanger [*P. volans*] is one of the most curious and pathetic babes that one can imagine with its lanky legs, very long tail and thin weedy body. Having outgrown the pouch, though still being nourished from it, the little phalanger clings to its mother's back during her nocturnal wanderings, though perhaps the gliding leaps are out of the question unless the youngster remains in the home tree or sleeping hollow'.

CONCLUSION

Petauroides volans has had a long and sometimes confusing taxonomic history. It has been listed as a member of 10 genera (*Belideus*, *Didelphis*, *Petaurista*, *Petaurides*, *Petauroides*, *Petaurus*, *Phalanger*, *Phalangista*, *Schinobates*, and *Voluccella*) and there have been at least 23 different binomial names used for it since its discovery. This geographically widespread species was sent to different museums throughout Europe by collectors, and given different designations by 19th Century zoologists. These early zoologists were often rivals, each of whom was more anxious to discover and name species, than to find out the habits of the species already known (Partington 1937). Consequently errors were made, and some of

these have persisted into the modern literature. For example, Flannery (1994) mistakenly lists Hepoona Roo (= *Petaurus australis*) as synonymous with *P. volans*.

Early descriptions of the morphology of *P. volans* such as its colouration, size and the presence of a gliding membrane, are given in broad general terms but nevertheless they do have value from a historical viewpoint. Dental descriptions in the early literature vary, and some confusion with the similarly structured dentition of *Pseudocheirus peregrinus* is evident. Early behavioural observations include the ability to glide, and that it is nocturnally active using tree hollows as den sites. The earliest records of occurrence were centred about the Sydney district. As the colony expanded so did its recorded range. Gould (1863) reported that its distribution was from Port Phillip (Victoria) to Moreton Bay (Qld), and this is reasonably accurate when compared to our understanding of its current range.

ACKNOWLEDGEMENTS

We wish to thank the library staff at the AM, Sydney; Natural History Museum, London; and the University of Wollongong. For translating French articles, we are grateful to Betty Hassen, and for translating German we acknowledge Peter Simmons. We also thank Sandy Ingleby for access to the mammal collection in the AM, and Cécile Callou for correspondence and a photograph regarding a specimen from the MNHN. Finally, we owe a debt of gratitude to Ross Goldingay and Rob Whelan for helpful discussion and comments on earlier versions of the manuscript, and also to two anonymous referees for their advice.

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